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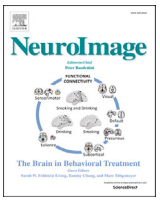

The sensation of groove engages motor and reward networks

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ABSTRACT

The sensation of groove has been defined as the pleasurable desire to move to music, suggesting that both motor timing and reward processes are involved in this experience. Although many studies have investigated rhythmic timing and musical reward separately, none have examined whether the associated cortical and subcortical networks are engaged while participants listen to groove-based music. In the current study, musicians and non-musicians listened to and rated experimentally controlled groove-based stimuli while undergoing functional magnetic resonance imaging. Medium complexity rhythms elicited higher ratings of pleasure and wanting to move and were associated with activity in regions linked to beat perception and reward, as well as prefrontal and parietal regions implicated in generating and updating stimuli-based expectations. Activity in basal ganglia regions of interest, including the nucleus accumbens, caudate and putamen, was associated with ratings of pleasure and wanting to move, supporting their important role in the sensation of groove. We propose a model in which different cortico-striatal circuits interact to support the mechanisms underlying groove, including internal generation of the beat, beat-based expectations, and expectation-based affect. These results show that the sensation of groove is supported by motor and reward networks in the brain and, along with our proposed model, suggest that the basal ganglia are crucial nodes in networks that interact to generate this powerful response to music.

1. Introduction

The sensation of groove, defined as the pleasurable desire to move to music (Janata et al., 2012), is one of the most powerful sources of music-derived pleasure. One way in which music is thought to elicit pleasure is through the interplay between the violation and fulfillment of musical expectations (Cheung et al., 2019; Huron, 2006; Juslin and Västfjäll, 2008; Meyer, 1956; Salimpoor et al., 2015). Musicians and composers can manipulate the expectations of a listener by altering the complexity or predictability of the rhythms, melodies, harmonies, or other factors that make up a piece of music. For example, listeners prefer melodies that are moderately complex (i.e., moderately unpredictable) compared to very simple or very complex melodies (Pearce and Wiggins, 2012). Similarly, groove is thought to rely predominantly on rhythmic expectations, with moderately complex rhythms leading to greater pleasure and wanting to move (Matthews et al., 2019; Sioros et al., 2014; Witek et al., 2014).

Rhythmic expectations are closely tied to the metre, which is the pattern of alternating strong and weak beats (London, 2012; Vuust and Witek, 2014). For example, in a waltz metre which consists of a strong beat followed by two weak beats, listeners will expect a note to fall on the strong beat. When notes fall between beats, or on weak beats rather than strong beats, they create syncopations which violate expectations and challenge the metre (Fitch and Rosenfeld, 2007; Vuust and Witek, 2014). Very simple rhythms with no syncopations are highly predictable, but boring, as most, if not all rhythmic expectations are confirmed. Highly complex rhythms, with many syncopations, are unpredictable and hard to follow as it is difficult for the listener to perceive a metre, and thus generate rhythmic expectations. Medium complexity rhythms, with some syncopations, strike a balance allowing for both the formation and

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violation of rhythmic expectations. As the metre is challenged by syncopations, rhythmic expectations need to be assessed and updated. It has been proposed that this continuous engagement of rhythm expectation processes drives the pleasure associated with groove (Koelsch et al., 2019; Vuust et al., 2018; Vuust and Witek, 2014). One way of assessing rhythmic expectations is through movement (Patel and Iversen, 2014), which may account for the desire to move associated with groove (Koelsch et al., 2019).

The link between rhythmic expectations and wanting to move suggests that motor regions of the brain may be involved in processing groove-based music such as funk, Afro-Cuban, and hip-hop (Danielsen, 2006; Greenwald, 2002). There have been no previous neuroimaging studies investigating the brain regions involved in the sensation of groove. However, studies of beat perception show activity in brain networks associated with auditory-motor integration and motor timing (Araneda et al., 2016; Bengtsson et al., 2009; Burunat et al., 2017; Chapin et al., 2010b; Chen et al., 2008; Grahn and Brett, 2007; Grahn and Rowe, 2013, 2009; Kung et al., 2013; Schubotz et al., 2000; Thaut et al., 2014). The basal ganglia (BG) seem to be particularly important for beat perception as they are crucial nodes in a core timing network proposed to underlie beat-based timing (Matell and Meck, 2004; Merchant et al., 2015; Teki et al., 2011). The BG also form distinct cortico-striatal circuits that may support different motor and motivational functions relevant to groove (Alexander et al., 1986; Haber, 2003). Recent studies have demonstrated that the putamen and supplementary motor area (SMA), which are parts of the cortico-striatal 'motor circuit', show selective responses to beat and metre (Araneda et al., 2016; Li et al., 2019). The caudate forms circuits with both prefrontal and parietal regions (Jarbo and Verstynen, 2015) and has been implicated in both rhythmic (Trost et al., 2014) and harmonic expectations (Seger et al., 2013).

Premotor, prefrontal, and parietal regions are also often activated in response to a strong beat (Bengtsson et al., 2009; Danielsen et al., 2014; Grahn and Schuit, 2012; Grahn et al., 2011; Grahn and McAuley, 2009; Grahn and Rowe, 2009; McAuley et al., 2012; Schubotz et al., 2000; Schubotz and von Cramon, 2001). These regions are part of the dorsal auditory stream (Hickok and Poeppel, 2004; Rauschecker, 2011), while premotor and parietal regions together form the dorsal fronto-parietal network (Ptak et al., 2017). These networks are believed to underlie abstract motor representations that allow for integration of sensory information over time (Ptak et al., 2017; Rauschecker, 2011). Furthermore, rhythmic expectations can be thought of as temporal predictions which are thought to originate in the motor and premotor cortices (Morillon and Baillet, 2017; Rimmele et al., 2018) and may reflect covert action simulation (Arnal, 2012; Patel and Iversen, 2014; Ross et al., 2016; Schubotz, 2007). Therefore, groove may activate motor regions of the brain via both the motor processes underlying rhythmic expectations and the overt or covert movement preparation purportedly involved in testing these expectations. Consistent with this, motor cortical excitability has been found to be greater for high compared to low groove music (Stupacher et al., 2013).

In addition to their role in beat-based timing, the BG, particularly the caudate and nucleus accumbens (NAcc), are associated with the anticipation and experience of music-derived pleasure (Blood et al., 1999; Blood and Zatorre, 2001; Koelsch, 2014; Salimpoor et al., 2013, 2011). Activity in the NAcc has been associated with the experience of pleasure including from primary (e.g., food and sex) and secondary (e.g., money) rewards (Sescousse et al., 2013). During music-listening, the NAcc is active during moments of peak pleasure, while the caudate is active in the period just before peak pleasure, suggesting that the caudate is involved in the anticipation of pleasure (Salimpoor et al., 2011). The medial orbitofrontal cortex (mOFC) also plays a role in assigning, maintaining and monitoring the value of a stimulus (Kringelbach, 2005; O'Doherty, 2004), including music (Koelsch, 2014). A network formed by the NAcc, mOFC, and auditory cortex has been linked to the enjoyment of music as shown by both structural (Martinez-Molina et al., 2019) and functional (Salimpoor et al., 2013) connectivity measures.

Taken together, the sensation of groove can be framed as the intersection of reward processing and the motor processes that underlie beat perception, with rhythmic expectations as the driving mechanism. Therefore, to test the role of both reward and motor networks in the experience of groove, we asked participants to listen to rhythms with medium and high levels of complexity (i.e., degree of syncopation), and rate both their desire to move and pleasure while undergoing functional magnetic resonance imaging (fMRI). Stimuli were drawn from a previous behavioural study showing that medium complexity rhythms were rated as more pleasurable and elicited a greater desire to move compared to low and high complexity rhythms (Matthews et al., 2019). Because we also found that harmonic complexity modulated the affective component of groove, this factor was included here. Finally, we tested both musicians and non-musicians based on evidence that training can affect both the sensation of groove (Matthews et al., 2019; Senn et al., 2018) and neural processing in both auditory-motor (Alluri et al., 2017; Grahn and Brett, 2007; Grahn and Rowe, 2009) and reward networks (Alluri et al., 2015; Chapin et al., 2010a).

We expected medium complexity stimuli to elicit activation in brain networks involved in the processing of musical beat, as well as in cortical and striatal regions linked to reward, with stronger effects in musicians than non-musicians. Given the roles of the putamen, caudate, and NAcc in beat-based timing and reward, we focused analysis on these regions of interest.

2. Material and methods

2.1. Participants

Fifty-seven participants were recruited into two groups (musicians and non-musicians). Musicians had a minimum of eight years of training and were currently practicing. Non-musicians had less than one year of training and were not currently practicing. Informed consent was obtained, and the study was approved by the Central Denmark Region Committees on Health Research Ethics. Participants received 200 DKK remuneration. Two non-musicians were excluded from the scanning session due to technical problems. Another non-musician was excluded as their ratings showed no variability. Demographic data for the final sample are provided in Table 1.

2.2. Stimuli

The stimuli were a subset of those developed and validated in a previously reported online study (Matthews et al., 2019). The stimuli consisted of short musical sequences with two levels of both rhythmic and harmonic complexity. There were three rhythms and three chords for each level of complexity resulting in 36 unique stimuli of four different categories: medium rhythm/medium harmony (Mr-Mh), medium rhythm/high harmony (Mr-Hh), high rhythm/medium harmony (Hr-Mh), and high rhythm/high harmony (Hr-Hh). These levels of complexity were chosen since, in the previous study, medium levels of rhythmic and harmonic complexity elicited the highest ratings and showed the greatest difference in ratings compared to high complexity rhythms and chords. In addition, two rather than three levels of complexity were chosen in order to maximize the number of trials for each level. The stimuli were created using Cubase Pro version 8.0.30 (Steinberg Media Technologies).

The sequences consisted of piano chords organized into rhythmic chord patterns in a piano timbre presented at 96 beats per minute. Each

Table 1
Participant demographic data.

	Non-Musicians	Musicians
N (male/female)	25 (13/12)	29 (17/12)
Age (SD)	23.20 (2.46).	23.76 (2.84)
Years of musical training (SD)	0.16 (0.31)	11.5 (3.27)
Hours of music practice per week (SD)		11.67 (10.20)

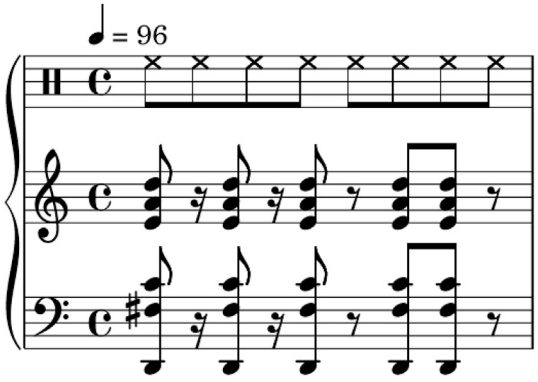

Fig. 1. Example of a stimulus with medium levels of rhythmic and harmonic complexity.

sequence was 10 s long and contained four repeats of a five-onset rhythm pattern with a single chord repeating throughout each sequence plus an isochronous eighth-note hi-hat pattern (see Fig. 1 for musical notation of a medium complexity rhythm and SFig. 1 for a schematized representation of all rhythm patterns). The medium complexity rhythms consisted of two Afro-Cuban rhythms known as the son clave and rumba clave, and one experimenter-created rhythm. The high complexity rhythms had all but the first onsets shifted to be early or late relative to the medium complexity patterns, thus increasing their rhythmic complexity. Rhythmic complexity was quantified using the syncopation index (Fitch and Rosenfeld, 2007). As the hi-hat pattern was identical for all stimuli, it was not included when calculating the syncopation index. C-scores – a measure of counter-evidence to the metre – (Povel and Essens, 1985) were also calculated for each rhythm and were consistent with the syncopation index within each level of complexity (see SFig. 2A and 2B).

All chords were in the key of D major and included six notes spanning four octaves (D2 to D#5; see Fig. 1 for musical notation of a medium complexity chord and Table S1 for a list of notes and corresponding frequencies for all chords). In musical terms, the medium complexity chords consisted of four-note chords with extensions. High complexity chords included a flat ninth interval between chord note and extension which is considered highly dissonant, when not specifically occurring as a flat 9th on a major 7th chord, according to contemporary harmonic theory (Freeman and Pease, 1989; Levine, 2011; Nettles and Ulanowsky, 1987). In lay terms, the high complexity chords contained notes with frequencies, or multiples of frequencies, that were very close to each other, thus creating an unpleasant sense of roughness or dissonance, while the medium complexity chords did not. Harmonic complexity was quantified using measures of peak roughness and inharmonicity, calculated using the MIRtoolbox version 1.6.1 (Lartillot et al., 2007; see SFig. 1D and 1C;).

2.3. Procedure

Before arriving for the study, participants filled out a questionnaire about their musical background and demographic information. Upon arrival, participants were familiarized with the stimuli and rating task with four familiarization trials using stimuli that were not included in the main study. There were two sessions during which participants listened to and rated all 36 stimuli, one inside the fMRI scanner and one outside the scanner. In order to avoid having ratings of wanting to move and pleasure influence each other, participants rated wanting to move in the scanner then pleasure and beat strength outside of the scanner, always in this order. Ratings of beat strength were collected in order to substantiate the rhythmic complexity manipulation and to investigate the association between the sensation of groove and perception of beat strength. In the scanning session, participants underwent three fMRI runs, each lasting around 11 min, during which they listened to all 36 stimuli in a pseudo-random order. A randomly selected subset of 12 stimuli were rated in each scanning run so that all 36 stimuli were rated over the three runs. Rating trials were randomly distributed within each run and participants were not aware that a given sequence would be rated until after it was presented, thus avoiding rating-specific activations. Participants selected their rating on a five-point visual scale by pressing two buttons on a button box to move a cursor right or left along the rating scale. Participants had 7 s to make their rating and non-rated trials had inter-stimulus intervals of five, 7.5, or 10 s. Participants were instructed to look at a fixation cross while sequences were presented.

In order to reduce the effect of scanner noise, stimuli were presented with noise reduction headphones (Opto-Active, OptoAcoustics, Mazor, Israel, http://www.optoacoustics.com/me dical/optoactive/features). In addition, participants wore earplugs inside the headphones. In order to compensate for the low-pass filter effect of the earplugs, the stimuli were compared with and without earplugs and then altered so that they subjectively matched. This resulted in a 10–20 dB increase for frequencies greater than 1500 Hz. This adjustment was identical for all stimuli and participants.

After the scanning, participants listened to the stimuli again while seated at a computer. After each sequence participants had 10 s to rate the degree of pleasure they experienced and the beat strength of the sequence, both on a five-point visual scale, using a computer mouse to select their rating.

2.4. Behavioural data analysis

Correlations between rating types were tested on participants' averaged ratings (one value per participant). Confidence intervals around correlation coefficients were calculated via bootstrapping with 5000 iterations. Analysis of the effects of rhythmic and harmonic complexity and group on ratings of pleasure, wanting to move, and beat strength were conducted on trial-level ratings using linear mixed effects regression with the lme4 package (Bates et al., 2014) in R (version 3.4.1, R core team, 2017). A linear mixed effects approach was used to account for inter-individual differences in ratings and in the effects of rhythmic and harmonic complexity as well as differences in effects across the three rhythms and chords (referred to as items) within each level of complexity. Starting with the maximal random structure, including by-participant and by-item random slopes and intercepts, this structure was then reduced to the optimal structure that could be supported by the data following the steps of Bates et al. (2015) and using their RePsychLing package. This led to by-participant random slopes and intercepts for rhythmic and harmonic complexity in all three models and by-item random intercepts for the models with wanting to move and beat ratings as outcome variables.

For the effects of interest, a forward hierarchical approach was used whereby regressors were added incrementally to an intercept-only model, then tested for increases in fit using the likelihood ratio test. Regressors that significantly contributed to model fit were included in a final model (fit with restricted maximum likelihood criterion) which was used to get parameter estimates of these regressors. For interactions, estimates of means and mean differences were calculated using emmeans (Lenth et al., 2018). Confidence intervals around the parameter estimates were calculated via parametric bootstrapping with 5000 iterations. Diagnostic plots of the residuals from all models were inspected for violations of the assumptions of normality and homoscedasticity. No violations were detected.

2.5. MRI data acquisition

Scanning took place at Aarhus University Hospital on a 3T Siemens TIM Trio scanner with a 32-channel coil. Each participant underwent three runs of whole-brain echo-planar imaging (EPI) using a multi-echo sequence which involved acquiring two whole brain volumes at two different echo times (TE1 = 12.4 ms, TE2 = 27.92 ms) per repetition time (TR = 2000 ms and voxel size = 2.35 × 2.53 × 2.50 mm, number of

slices = 54, flip angle = 78°). Using the multi-echo sequence reduces signal drop out in regions near sinuses such as the orbitofrontal cortex. The two EPI images within each TR were combined using a signal-to-noise ratio weighted average. This resulted in 326 images per run, with a total of 978 images per participant. T1 structural images were collected for each participant at the start of each session (TR = 2420 ms, TE = 3.7 ms, voxel size = 1 mm iso, flip angle = 9°).

2.6. MRI preprocessing and statistical analysis

Statistical Parametric Mapping software (SPM12 Wellcome Trust Centre for Neuroimaging, University College London; www.fil.ion.ucl.ac.uk/spm/) was used for preprocessing and statistical analysis. Standard preprocessing steps were followed, including slice timing correction, unwarping, motion correction, coregistration to an MNI template, segmentation, spatial normalization, and spatial smoothing with an 8 mm FWHM kernel.

First-level analysis used the general linear model with four condition regressors corresponding to the four types of stimuli (Mr-Mh, Mr-Hh, Hr-Mh, Hr-Hh) as well as twenty-four regressors accounting for motion parameters, and an additional regressor accounting for rating responses which were modeled as events time-locked to button presses. Silent inter-stimulus intervals were unmodeled, thus acting as an implicit baseline. All regressors were then convolved with a canonical hemodynamic response function. Four contrast images were calculated per participant, corresponding to the four stimuli conditions. These were then entered into a second level analysis where group-level contrasts for each main effect and interaction were generated. All results are reported at a false discovery rate (FDR; peak-level) corrected $p < .05$. In a mixed design, SPM uses the same error term and degrees of freedom for main effects of both within and between-subject factors (Chen et al., 2014; McLaren et al., 2011). Therefore, a confirmatory analysis was implemented in GLM Flex (http://mrtools.mgh.harvard.edu/index.php/GLM_Flex) with the same contrasts and FDR correction (see Tables S2–S4 for results).

2.7. Region of interest analyses

Parameter estimates (betas) for each participant, for each condition were extracted from the putamen and caudate (left and right combined) as well as the left and right nucleus accumbens using Marsbar (Brett et al., 2002; http://marsbar.sourceforge.net/) with anatomical masks from a probabilistic atlas (Hammers et al., 2003). Effects of rhythmic and harmonic complexity and musical training were then assessed using the same approach as the analysis of the ratings. Only by-participant random effects were included since parameter estimates were extracted from group level contrast images which did not contain item (i.e., trial) level activations.

An additional analysis was implemented to investigate the relation between subjective ratings and ROI activity. This analysis also used hierarchical linear mixed effects regression, with parameter estimates from the ROIs as outcome measures, and group, beat strength ratings, pleasure ratings, and wanting to move ratings, as well as interactions between group and the three types of ratings, as predictors. As in the above analysis, only by-participant random effects were included. In order to assess the degree of overlap in variance accounted for by pleasure and wanting to move ratings, and whether they accounted for variance over and above beat strength ratings and group differences, the hierarchical regression was implemented with two different orders: 1. Group, beat strength ratings, pleasure ratings, and wanting to move ratings, and 2. Group, beat strength ratings, wanting to move ratings, and pleasure ratings. The interactions between group and the ratings were entered after the main effects and followed the same orders. In addition to the final models including only the significant predictors from each hierarchical analysis, models with only pleasure ratings, only wanting to move ratings, and both together as predictors, were assessed.

Based on the findings of the whole brain analysis, a post hoc analysis was implemented to investigate the effect of rhythmic and harmonic complexity as well as the three ratings types on mOFC activity. The mOFC ROI was generated from the any effect whole brain F-contrast (thresholded at $p < 0.05$, FDR) and included two clusters on the left with peaks at x = −18, y = 28, z = -18 and x = −14, y = 42, z = −20 and one cluster on the right with two peaks at x = 24, y = 32, z = −12, and x = 26, y = 32, z = −22. The parameter estimates from this ROI were submitted to two analyses identical to those carried out on the BG ROIs.

The subjective ratings, background data, relevant t-maps, extracted ROI activations that support these findings, as well as the python code for generating stimuli orders, presenting stimuli, and recording responses, are available in the Open Science Framework with identifier link: https://doi.org/10.17605/osf.io/z2sy9.

3. Results

3.1. Behavioural results

All three types of ratings were strongly correlated yet independent enough to be analyzed separately: Pleasure and wanting to move ratings ($r = 0.62$, 95% CI[0.36, 0.81]); pleasure and beat strength ratings ($r = 0.55$, 95% CI[0.27, 0.77]); Wanting to move and beat strength ratings ($r = 0.42$, 95% CI[0.19, 0.61]).

For both musicians and non-musicians, pleasure ratings decreased as rhythmic and harmonic complexity increased (Fig. 2A). However, a significant interaction between rhythmic and harmonic complexity ($\chi^2(1) = 8.98$, $p < .003$) showed that the difference in ratings between Mr-Mh and Mr-Hh (mean difference (MD) = 0.696) was greater than the difference between Hr-Mh and Hr-Hh (MD = 0.440; $b = 0.250$, 95% CI [0.090, 0.409]). This suggests that medium complexity chords increased pleasure to a greater degree when combined with medium complexity rhythms compared to high complexity rhythms. The rhythm by group interaction improved model fit ($\chi^2(1) = 4.69$, $p = .030$) and showed that the difference in ratings between medium and high complexity was greater for non-musicians (MD = 1.53) than musicians (MD = 1.17; $b = -0.364$, 95% CI[-0.679, −0.035]).

For wanting to move ratings, there was a three-way interaction with rhythm, harmony, and group ($\chi^2(1) = 5.84$, $p = .016$; Fig. 2B). Musicians showed a greater difference in ratings between Mr-Mh and Mr-Hh (MD = 0.521) compared to Hr-Mh and Hr-Hh (MD = 0.226) whereas for non-musicians, the differences between Mr-Mh and Mr-Hh (MD = 0.116) and Hr-Mh and Hr-Hh (MD = 0.151) were similarly small ($b = 0.331$, 95% CI[0.062, 0.601]). This suggests that musicians' wanting to move ratings were increased by the combination of medium complexity rhythms and chords whereas non-musicians' ratings were increased by medium complexity rhythms alone.

For beat strength, the main effect of rhythmic complexity significantly improved model fit ($\chi^2(1) = 74.83$, $p < .001$), with medium complexity rhythms rated as having a stronger beat than high complexity rhythms ($b = 1.672$, 95% CI[1.408, 1.933]). The rhythm by harmony interaction also improved model fit ($\chi^2(1) = 4.08$, $p = .043$) showing that Hr-Mh were rated as having higher beat strength than Hr-Hh (MD = 0.207), whereas Mr-Mh and Mr-Hh were rated more similarly (MD = 0.077; $b = -0.130$, 95% CI[-0.254, 0.002]; Fig. 2C). This suggests that high complexity rhythms combined with medium complexity chords are rated as having higher beat strength than high complexity rhythms with high complexity chords. However, the confidence interval contains zero suggesting that this effect may be unstable. There was no significant main effect of group nor a significant interaction between group and rhythmic and/or harmonic complexity.

3.2. Whole-brain fMRI results

Whole-brain contrast images were used to assess the effects of rhythm, harmony, and musical training (group). Contrasting medium versus high complexity rhythms (medium > high complexity) revealed

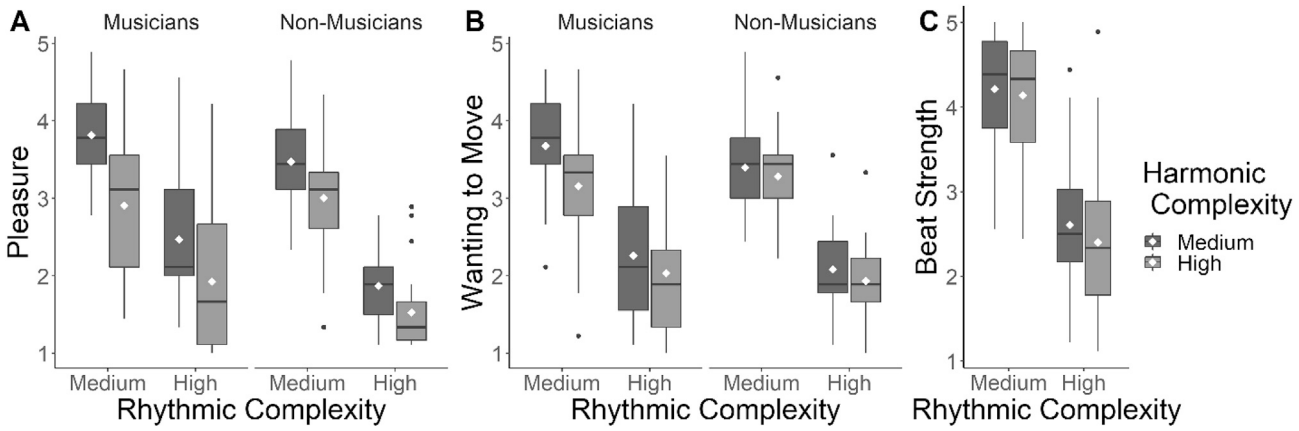

Fig. 2. Subjective ratings as a function of rhythmic complexity, harmonic complexity and group. **A.** Pleasure ratings. **B.** Wanting to move ratings. **C.** Ratings of beat strength. Center line, median; white dots, means; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; black dots, outliers.

Table 2
Stereotaxic Locations of Peak Voxels in the Medium > High Rhythmic Complexity Contrast. Peak activations thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Brain region	Cluster size	t(208)	*p*FDR	x	y	z
L putamen	345	5.53	0.004	−14	10	−2
L thalamus		3.61	0.026	−2	−2	8
R putamen	344	5.32	0.004	22	4	8
L inferior parietal lobule	681	4.72	0.007	−42	−48	44
		4.57	0.008	−28	−58	40
		4.35	0.01	−36	−54	40
L SMA	321	4.57	0.008	−6	20	48
		4.31	0.01	−4	12	52
L inferior temporal gyrus	153	4.53	0.008	−58	−40	−18
R angular gyrus	557	4.34	0.01	38	−58	50
R superior parietal lobule		4.32	0.01	34	−66	56
R angular gyrus		4.16	0.011	36	−50	38
L superior frontal gyrus	59	4.32	0.01	−24	14	68
L SMA	210	4.27	0.01	−8	−10	60
R SMA		3.64	0.025	8	−4	68
R middle frontal gyrus	95	4.2	0.011	34	6	52
R inferior temporal	50	3.97	0.015	58	−36	−16
L cerebellum, Crus1	74	3.93	0.015	−14	−92	−22
L inferior frontal pars triangularis	272	3.87	0.017	−40	26	28
L middle frontal gyrus		3.81	0.019	−38	36	16
R cerebellum, Crus 2	22	3.71	0.022	38	−68	−46
R pons	1	3.57	0.028	6	−20	−44
Calcarine sulcus	18	3.54	0.029	0	−82	−12
L superior frontal gyrus	8	3.51	0.03	−20	64	0
L middle frontal gyrus	13	3.47	0.032	−28	0	50
L superior parietal lobule	16	3.46	0.032	−32	−60	62
L medial orbital gyrus	18	3.46	0.033	−14	26	−22
L anterior orbital gyrus		3.36	0.039	−22	24	−22
L anterior cingulum	3	3.41	0.036	−12	32	28
L precentral gyrus	8	3.4	0.036	−16	−18	72
R mid cingulum	21	3.34	0.039	4	−4	30
L precentral gyrus	31	3.34	0.04	−46	8	32
R cerebellum, Crus 2	5	3.33	0.04	12	−88	−28
L frontal superior gyrus	1	3.27	0.044	−16	66	2
R inferior temporal	2	3.27	0.044	42	−50	−8
L precentral gyrus	3	3.26	0.045	−36	6	46
L frontal operculum	1	3.21	0.048	−46	14	2

activations in the bilateral BG including the putamen, caudate, and pallidum, with activation in the left BG bordering the NAcc. This contrast also revealed activation in a network of cortical regions associated with beat perception including the left SMA (including pre-SMA), bilateral dorsal premotor regions, and bilateral parietal regions (see Table 2 and Fig. 3). In addition, this contrast revealed significant activation in the left prefrontal cortex, left mOFC, the bilateral inferior temporal cortex, and crus 1 in the right cerebellum. The opposite contrast (high > medium complexity rhythms) revealed no significant activations. Contrasting musicians versus non-musicians (musicians > non-musicians; averaging over all stimuli conditions) revealed activations in the bilateral caudate, bilateral motor cortex (extending into dorsal premotor cortices), bilateral SMA, right prefrontal cortex, right Heschl's gyrus, and left posterior superior temporal gyrus (see Table 3 and Fig. 4). There were no significant activations in the reverse contrast (non-musicians > musicians), nor activations related to harmonic complexity, nor interactions between rhythmic and harmonic complexity or group.

3.3. ROI results

Activity in the right NAcc showed a rhythm by harmony interaction ($\chi^2(1) = 6.50$, $p = .011$). The difference between activation for Mr-Mh versus Mr-Hh (MD = 0.132) was greater than Hr-Mh versus Hr-Hh (MD = −0.063; $b = 0.195$, 95% CI[0.048, 0.343]; Fig. 5B) showing that the largest activation was for stimuli with medium complexity rhythms combined with medium complexity chords. Activity in the left NAcc showed a main effect of rhythmic complexity ($\chi^2(1) = 3.99$, $p = .046$) with greater activation for medium compared to high complexity rhythms ($b = 0.074$, 95% CI[0.001, 0.148]; Fig. 5C). Activity in the caudate showed main effects for both rhythmic complexity ($\chi^2(1) = 12.43$, $p < .001$) and group ($\chi^2(1) = 5.48$, $p = .019$), with greater activation for medium compared to high complexity rhythms ($b = 0.083$, 95% CI[0.038, 0.129]; Fig. 5D) and greater activation in musicians compared to non-musicians ($b = 0.184$, 95% CI[0.030, 0.337]). Activity in the putamen also showed a main effect of rhythmic complexity ($\chi^2(1) = 5.93$, $p = .015$), with greater activation for medium compared to high complexity rhythms ($b = 0.073$, 95% CI[0.015, 0.129]; Fig. 5E). In a post-hoc analysis, activity in the mOFC also showed a main effect of rhythmic complexity ($\chi^2(1) = 6.67$, $p = .01$), with greater activation for medium compared to high complexity rhythms ($b = 0.063$, 95% CI[0.015, 0.111]).

In order to assess the overlap in variance accounted for in the ROI activations by pleasure and wanting to move ratings, the hierarchical regression was implemented twice per ROI, once with pleasure added to the model first and once with wanting to move ratings added first (see Table 4 for results). In addition, final models with both the significant predictors from the hierarchical analyses as well as models with both wanting to move and pleasure as predictors, both alone and together, were assessed (see Table 5 for results and Fig. 6 for summary).

Analyses on the right NAcc activations showed that pleasure and wanting to move ratings accounted for overlapping variance, but only pleasure ratings accounted for variance over and above that of beat strength ratings. For the left NAcc activations, both pleasure and wanting to move ratings accounted for variance over and above beat strength

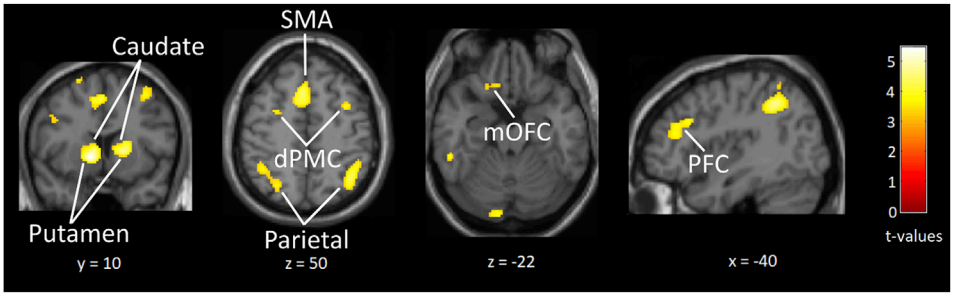

Fig. 3. Results of the medium > high rhythmic complexity contrast. dPMC, dorsal premotor cortex; mOFC, medial orbitofrontal cortex; PFC, prefrontal cortex; SMA, supplementary motor area. Images are thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Table 3
Stereotaxic Locations of Peak Voxels in the Musicians > Non-Musicians Contrast. Peak activations thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Brain region	Cluster size	t(208)	*p*FDR	x	y	z
L precentral gyrus	162	6.1	0	−46	−4	54
White matter	89	4.84	0.004	−38	−42	20
White matter		4.44	0.015	−40	−44	12
R precentral gyrus	105	4.33	0.018	46	−6	48
L SMA	101	4.24	0.023	−2	2	64
R inferior frontal pars triangularis	63	4.19	0.024	44	18	24
R Heschl's gyrus	8	4.16	0.025	56	−8	6
L caudate	55	4.04	0.031	−4	12	4
L superior temporal gyrus	43	4.01	0.032	−58	−48	18
White matter	15	3.98	0.033	22	−12	32
R supramarginal gyrus	3	3.73	0.045	56	−36	26

ratings, but the variance they accounted for was strongly overlapping. For activity in the caudate, wanting to move but not pleasure ratings, accounted for variance over and above beat strength ratings. A near-significant trend showed that wanting to move ratings accounted for marginally unique variance compared to pleasure ratings. Analyses on the putamen activations showed that wanting to move ratings accounted for unique variance over and above that accounted for by both beat strength and pleasure ratings. In addition, there was an interaction between group by beat strength ratings, however, due to overlapping variance accounted for, the nature of this interaction depended on the inclusion of wanting to move ratings. Finally, in the mOFC, results showed that wanting to move ratings accounted for variance over and above pleasure ratings. In the final models, wanting to move ratings accounted for unique variance, however, this affect only approached significance.

4. Discussion

In this study we set out to understand the brain networks involved in the sensation of groove. Consistent with previous findings, participants experienced a stronger sensation of groove for medium compared to high levels of both rhythmic and harmonic complexity, with higher ratings of pleasure and wanting to move (Matthews et al., 2019). This was coupled with greater activity for medium complexity rhythms in reward-related regions including the NAcc, caudate, and mOFC, and in regions associated with beat-based timing including the putamen, SMA, as well as prefrontal and parietal cortices. In addition, in both the left and right NAcc, pleasure and wanting to move ratings predicted activity to a similar degree, largely accounting for the same variance. In the mOFC, there was overlap in variance accounted for by wanting to move and pleasure, however, wanting to move was a stronger predictor. In the putamen, wanting to move ratings accounted for variance over and above that accounted for by both pleasure and beat strength ratings. In the caudate, wanting to move ratings and beat strength ratings accounted for overlapping variance. Finally, musicians showed overall greater activity in regions associated with beat perception.

Together, these findings suggest that the sensation of groove is driven by a combination of motor and reward regions in the brain. We interpret these results in the context of rhythmic expectations, suggesting that the generation of these expectations based on a regular beat, and their

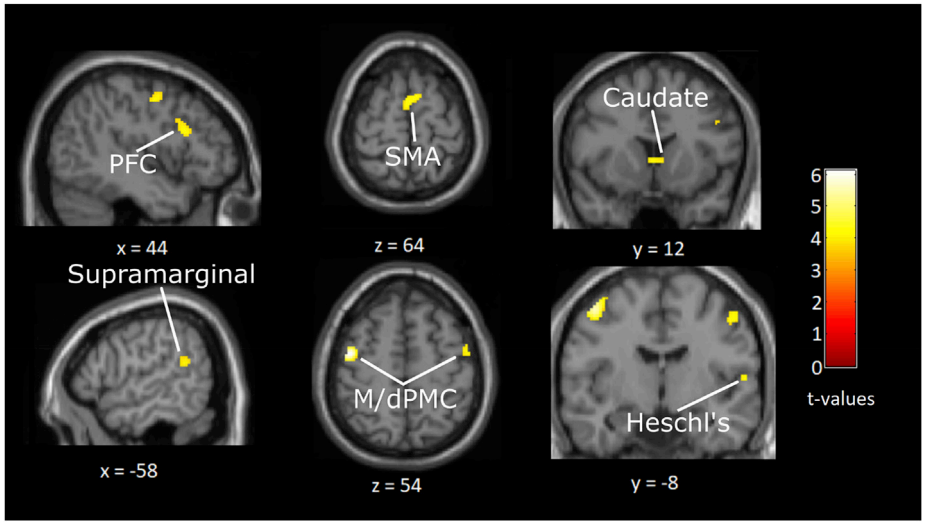

Fig. 4. Results of the musician > non-musician contrast. M/dPMC, motor/dorsal premotor cortex; PFC, prefrontal cortex; SMA, supplementary motor area. Images are thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

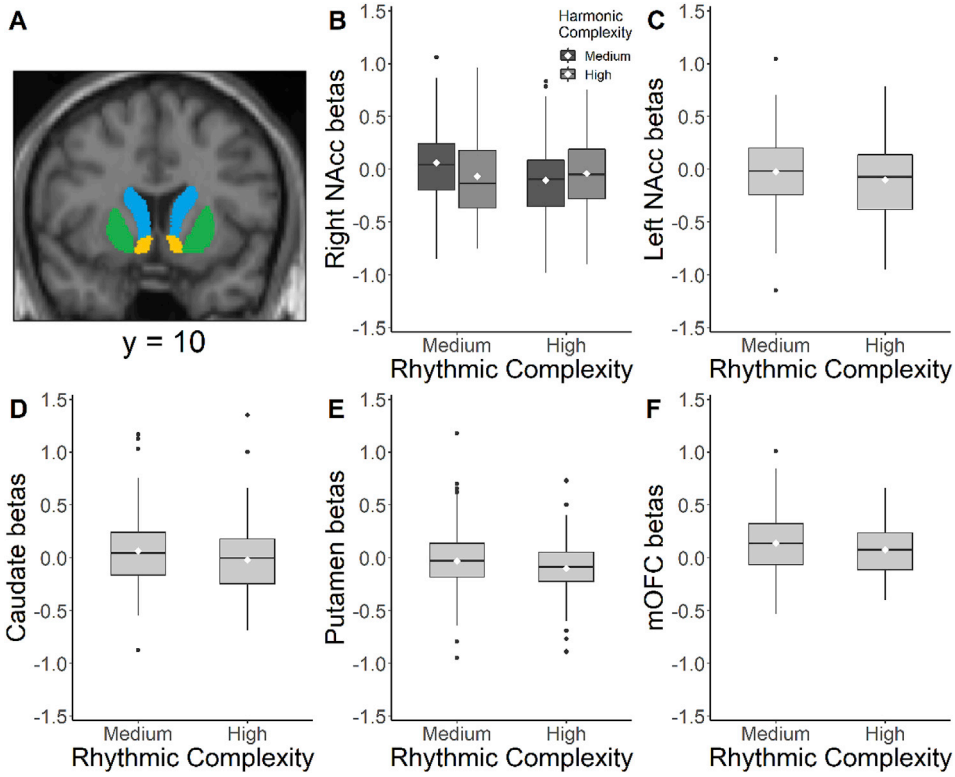

Fig. 5. Results of ROI analysis. **A.** Coronal view of a single subject MNI template showing BG masks from probabilistic anatomical atlas used in region of interest analyses (Hammers et al., 2003). Blue, caudate; Green, putamen; Orange, nucleus accumbens. **B.** Right nucleus accumbens activation as a function of rhythmic and harmonic complexity. **C.** Left nucleus accumbens activation as a function rhythmic complexity. **D.** Caudate activation as a function of rhythmic complexity. **E.** Putamen activation as a function of rhythmic complexity. **F.** Medial orbitofrontal cortex activation as a function of rhythmic complexity. NAcc, nucleus accumbens; mOFC, medial orbitofrontal. Center line, median; white dots, means; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; black dots, outliers.

violation via syncopations, are core drivers of groove (Matthews et al., 2019; Vuust and Witek, 2014). Based on this formulation, we propose a theoretical model of the brain mechanisms underlying groove that is centered on the cortico-striatal circuits thought to underlie predictive timing and reward processing.

4.1. Medium complexity rhythms drive the sensation of groove

Behavioural results showed that medium complexity rhythms led to higher ratings of pleasure, wanting to move, and beat strength. Only the medium and high complexity conditions were included in order to maximize the number of trials per condition. Therefore, we could not confirm an inverted U-shaped pattern of ratings here. However, ratings for the medium and high complexity rhythms are consistent with those obtained in our previous study which included the low complexity condition (Matthews et al., 2019). Therefore, the current results provide further evidence that medium complexity rhythms strongly contribute to the sensation of groove.

Consistent with previous results, medium complexity chords in combination with medium complexity rhythms increased pleasure ratings, providing further evidence that harmony enhances the affective component of groove (Matthews et al., 2019). Intriguingly, ratings of beat strength were also enhanced by medium complexity chords, supporting previous work showing that beat and metre perception are not driven by rhythmic factors alone (Dawe et al., 1993; Hannon et al., 2004). Finally, for musicians, the combination of medium complexity rhythms and chords enhanced the desire to move, suggesting that for those with musical training, the sensation of groove is more affected by non-rhythmic factors.

4.2. The sensation of groove involves reward regions of the brain

fMRI results showed that medium complexity rhythms were associated with greater activity in the left NAcc and left mOFC. Converging evidence from neuroimaging studies suggests that the NAcc and mOFC are important for the experience of music-derived pleasure (Koelsch, 2014; Martinez-Molina et al., 2019; Martínez-Molina et al., 2016; Salimpoor et al., 2013). Here, activity in both left and right NAcc also showed a positive association with both pleasure and wanting to move ratings, suggesting an association with groove overall rather than the pleasure component alone. One explanation may be that the NAcc is not only involved in the experience of music-derived pleasure, but also in the processing of expectations that can lead to such pleasure (Gebauer et al., 2012; Koelsch, 2014; Salimpoor et al., 2015). For example, NAcc activation has recently been associated with musical uncertainty (Cheung et al., 2019) and musical surprise (Shany et al., 2019), and has also been shown to track reward prediction errors associated with harmonic violations (Gold et al., 2019). In the current study, the right NAcc showed greater activation in response to the combination of medium complexity rhythms and chords, which was the condition that elicited the highest pleasure and wanting to move ratings. Interestingly, this was the only region to show an effect of harmonic complexity, which might relate to the right-dominance of regions involved in tonal processing (Zatorre et al., 2002).

Activity in the mOFC has been associated with assigning affective value to stimuli, including music (Zatorre and Salimpoor, 2013). However, in the current results mOFC activity showed a stronger association with wanting to move ratings than with pleasure ratings. A more recent hypothesis suggests that OFC involvement in value assignment is contingent on whether this process involves mental simulation of behavioural outcomes (Stalnaker et al., 2015). This is consistent with the current results as wanting to move ratings, in contrast to pleasure ratings, may involve action simulation. Therefore, one possibility is that the NAcc encodes the positive affective state of groove, while the mOFC encodes the association between the music and the desire to move.

4.3. The sensation of groove involves motor regions of the brain

Our results also showed greater activation in bilateral putamen and caudate as well as the SMA (including pre-SMA) and bilateral dorsal

Table 4
Results of Hierarchical Analysis Testing the Association between ROI Activations and Subjective Ratings.

Region	Order	Predictor	$\chi^2(1)$	p value
R NAcc				
		Group	2.165	0.141
		Beat	0.868	0.352
	Pleasure First	Pleasure	4.501	0.034
		Move	0.084	0.772
	Move first	Move	2.534	0.111
		Pleasure	2.050	0.152
L NAcc				
		Group	0.487	0.485
		Beat	2.649	0.104
	Pleasure First	Pleasure	4.172	0.041
		Move	1.751	0.186
	Move first	Move	5.389	0.020
		Pleasure	0.534	0.465
Caudate				
		Group	5.481	0.019
		Beat	4.956	0.026
	Pleasure First	Pleasure	2.812	0.094
		Move	3.636	0.057
	Move first	Move	6.448	0.011
		Pleasure	0.000	0.984
Putamen				
		Group	0.863	0.353
		Beat	1.607	0.205
	Pleasure First	Pleasure	3.499	0.061
		Move	3.913	0.048
		Group:beat	9.922	0.002
	Move first	Move	7.401	0.007
		Pleasure	0.011	0.917
mOFC				
		Group	2.510	0.113
		Beat	3.329	0.068
	Pleasure First	Pleasure	0.630	0.427
		Move	4.414	0.036
	Move first	Move	4.499	0.034
		Pleasure	0.546	0.460

Beat, beat strength ratings; Move, wanting to move ratings.
Pleasure, pleasure ratings; NAcc, nucleus accumbens.
mOFC, medial orbitofrontal cortex.

Table 5
Results of Final Models Testing the Association between ROI Activations and Subjective Ratings.

Region	Model	Predictor	β	95% CI
R NAcc				
	Pleasure		0.047	[0.004, 0.089]
	Move		0.042	[-0.004, 0.090]
	Pleasure and Move	Pleasure	0.055	[-0.026, 0.137]
		Move	−0.010	[-0.104, 0.082]
L NAcc				
	Pleasure		0.053	[0.015, 0.092]
	Move		0.062	[0.018, 0.107]
	Pleasure and Move	Pleasure	0.021	[-0.053, 0.094]
		Move	0.042	[-0.040, 0.123]
Caudate				
	Group and Beat	Group	0.182	[0.035, 0.335]
		Beat	0.026	[0.003, 0.049]
	Group, Beat, and Pleasure	Pleasure	0.035	[-0.006, 0.075]
	Group, Beat, and Move	Move	0.064	[0.014, 0.113]
	Group, Beat, Pleasure, and Move	Pleasure	−0.001	[-0.056, 0.053]
		Move	0.064	[-0.000, 0.132]
Putamen				
	Group:Beat		−0.073	[-0.120, −0.026]
	Group:Beat, and Pleasure	Pleasure	0.022	[-0.020, 0.063]
	Group:Beat, and Move	Move	0.061	[0.013, 0.109]
	Group:Beat, Pleasure, and Move	Pleasure	−0.023	[-0.080, 0.031]
		Move	0.079	[0.014, 0.145]
mOFC				
	Pleasure		0.028	[0.000, 0.057]
	Move		0.045	[0.016, 0.077]
	Pleasure and Move	Pleasure	−0.015	[-0.067, 0.036]
		Move	0.060	[-0.000, 0.119]

Beat, beat strength ratings; Move, wanting to move ratings.
Pleasure, pleasure ratings; NAcc, nucleus accumbens.
mOFC, medial orbitofrontal cortex. Group:Beat, a group by beat strength ratings interaction from models that also includes the main effect of each.

premotor cortices for medium complexity rhythms. The putamen and the SMA are part of the cortico-striatal 'motor circuit' (Alexander et al., 1986) and together with the caudate are suggested to be crucial nodes in both the striatal beat-frequency and pacemaker-accumulator models of timing (Coull et al., 2011; Matell and Meck, 2004; Merchant et al., 2013). In addition, recent theories suggest that temporal predictions are generated in the motor system via covert and unconscious action simulation (Arnal, 2012; Patel and Iversen, 2014; Rimmele et al., 2018; Ross et al., 2016; Schubotz, 2007). This is supported by a recent study showing that temporal predictions in the context of regular auditory stimuli are driven by motor signals to the auditory cortex (Morillon and Baillet, 2017). In the context of beat perception, the efferent signals of these covert actions may act as an internal representation of the beat, or 'pacing signal' (Kotz et al., 2016), informing beat-based expectations.

Converging evidence suggest that the putamen, SMA and dorsal premotor cortices are crucial for generating an internal representation of a beat (Araneda et al., 2016; Grahn and Brett, 2007; Grahn and Rowe, 2009; Merchant et al., 2015), with the putamen seeming particularly important (Grahn and Rowe, 2013). Studies with both Parkinson's disease (Grahn and Brett, 2009) and lesion patients (Nozaradan et al., 2017) also support the importance of the BG in beat perception. Furthermore, oscillatory activity in the SMA and putamen has been shown to entrain to frequencies denoting the beat and metre, respectively (Li et al., 2019). However, two recent studies using transcranial magnetic stimulation (TMS) support the role of the dorsal premotor cortex (Ross et al., 2018a) but not the SMA (Ross et al., 2018b) in beat perception.

Interestingly, the caudate was the only region of interest whose activity showed a main effect of beat strength ratings. However, further analysis revealed strong overlap between the effects of beat strength and wanting to move ratings in this region. Beat strength ratings did show a relation to putamen activity via an interaction with group, the nature of which also depended on the inclusion of wanting to move ratings in the model. Together these results provide further evidence that beat perception and motor activation are strongly linked, both in terms of subjective experience and neural underpinnings.

4.4. The sensation of groove involves frontoparietal networks

Medium complexity rhythms also elicited increased activation in bilateral parietal (with peaks in inferior and superior parietal lobules) and left prefrontal cortical regions. Parietal and prefrontal regions are components of both the dorsal auditory (Hickok and Poeppel, 2004; Rauschecker, 2011) and the fronto-parietal networks (Ptak et al., 2017), which are thought to underlie the motor representations of stimuli allowing for the processing of sensory input that evolves over time (Ptak et al., 2017; Rauschecker, 2011). These regions have also been implicated in the cognitive aspects of temporal and rhythmic processing including temporal attention (Bolger et al., 2014; Coull and Nobre, 2008; Coull et al., 2011; Davranche et al., 2011; Nobre and van Ede, 2017), encoding and retrieval of beat-based time intervals (Konoike et al., 2015, 2012), and rhythmic deviant detection (Lappe et al., 2016, 2013). A recent TMS study showed that down-regulating parietal activity disrupts perception of phase shifts of the beat (Ross et al., 2018b). These results are consistent with the parietal cortices purported role as the interface between motor-driven temporal predictions and sensory input (Rauschecker, 2011; Rimmele et al., 2018).

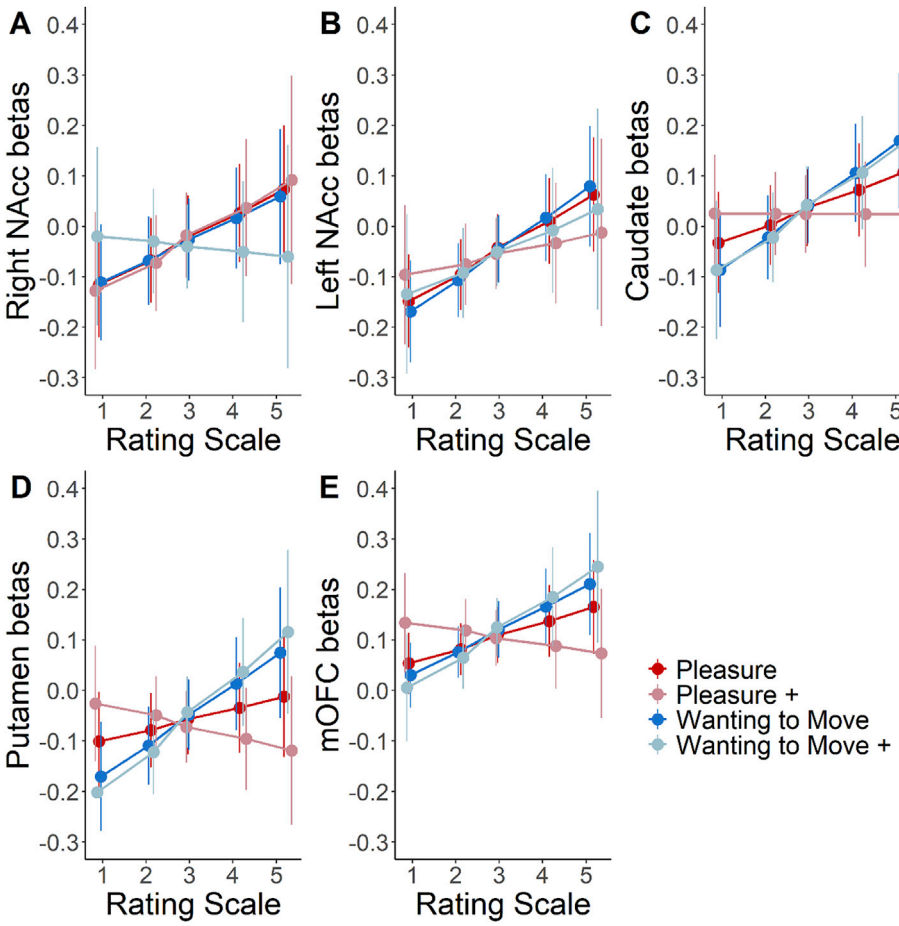

Fig. 6. Estimated means from regression models testing the effects of pleasure and wanting to move ratings on activation in the regions of interest. Pleasure + denotes models that also include wanting to move ratings and Wanting to Move + denotes models that also include pleasure ratings. Points on the graphs represent estimated mean activations for each rating on the five-point scale of the indicated rating type, while holding the other effects constant at their means. **A.** Right nucleus accumbens. Pleasure and Wanting to Move denote estimated means from models with only those predictors. **B.** Left nucleus accumbens. The models are identical to those in A. **C.** Caudate. All models also include group and beat strength ratings as predictors. **D.** Putamen. All models also include group and beat strength ratings as predictors, as well as an interaction between the two. **E.** Medial orbitofrontal cortex. The models are identical to those in A. NAcc, nucleus accumbens; mOFC, medial orbitofrontal cortex.

Prefrontal activity during beat perception has been linked to precision of sensory predictions (Bengtsson et al., 2009) and working memory (Kung et al., 2013), consistent with its role in beat-based timing (Teki et al., 2011). Therefore, the dorsal prefrontal activity seen here may represent the generation of beat-based expectations and monitoring of their outcome. The caudate is strongly connected to prefrontal and parietal regions (Haber, 2016), and both whole-brain and ROI analyses showed greater caudate activation for medium complexity rhythms. A recent study using TMS suggests that a left dorsolateral prefrontal-caudate circuit determines music liking and wanting by coding musical expectancies based on structural properties (Mas-herrero et al., 2018). In the current context, prefrontal and parietal regions, along with the caudate, may generate and update beat-based expectations and compare these expectations to incoming stimuli.

4.5. *Musicians show greater activation in regions associated with beat-based timing*

Although the overall pattern of activity was similar for both groups, musicians showed greater activity in the caudate, right prefrontal cortex, SMA, primary and premotor cortex and primary and secondary auditory regions, compared to non-musicians, regardless of rhythm complexity. Musicians have shown greater activity in the SMA and premotor cortex (Grahn and Brett, 2007) and greater connectivity between SMA and auditory regions (Grahn and Rowe, 2009) during rhythm perception tasks. Together, these results suggest that musical training leads to greater engagement of regions involved in beat perception as well as stronger auditory-motor associations (Alluri et al., 2017; Zatorre et al., 2007). This is in line with the current behavioural findings, as well as those from a previous study showing that musicians are more sensitive to rhythmic and harmonic manipulations (Matthews et al., 2019), and with results showing greater neural responses to rhythmic deviants (Geiser et al., 2010; Habibi et al., 2014; Vuust et al., 2009).

4.6. *A proposed model*

We propose a theoretical model integrating the current results with previous work discussed above. According to this model, the putamen, along with the SMA and premotor cortices automatically generate an internal representation of the beat. These regions interact with the caudate, prefrontal, and parietal regions which use this beat representation to inform rhythmic expectations and compare them to incoming stimuli. These regions may also use this beat information to generate higher-level expectations regarding the way music will unfold over longer timescales (Salimpoor et al., 2015). Information from both the putamen and caudate networks may then be passed to the NAcc-mOFC circuit which generates a positive affective response, including both pleasure and the desire to move, and assigns value to both rhythmic and higher-level expectations. Medium complexity rhythms activate these networks as they are regular enough to allow for internal beat generation, but also contain syncopations that challenge this regularity and thus engage expectation processes leading to the pleasurable desire to move. In addition, the repetition of rhythmic patterns, used here in our stimuli and common in groove-based music (Danielsen, 2006), may engage processes involved in higher-level expectations. Furthermore, musical training may strengthen these expectations and the brain networks that support them. Finally, although rhythm appears to be the primary feature influencing groove, other factors, including harmony and familiarity also enhance pleasure (Matthews et al., 2019; Pereira et al., 2011; Senn et al., 2019; van den Bosch et al., 2013).

5. Conclusion

The current study sought to investigate the brain networks underlying the pleasurable desire to move to music, known as the sensation of groove. Medium complexity rhythms led to greater activity in brain regions associated with both motor timing and reward. Subjective ratings of pleasure and wanting to move were associated with activity in BG regions of interest supporting their crucial role, not only in processing rhythmic complexity, but also in the subjective experience of groove. These results provide novel evidence supporting the formulation of groove as the intersection of motor timing and reward processes. Based on this formulation, we propose a model in which different cortico-striatal networks support the generation and affective valuation of beat-based expectations. Future studies will test the interactions between these networks, leading to a better understanding of how prediction and reward-based mechanisms work together.

Author contributions

Tomas E. Matthews: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Visualization, Project administration Maria A. G. Witek: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Writing - Review & editing, Project administration Torben Lund: Methodology, Software, Formal analysis, Resources, Data Curation Peter Vuust: Conceptualization, Methodology, Writing - Review & editing, Supervision Virginia B. Penhune: Conceptualization, Methodology, Writing - Review & editing, Supervision.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116768.

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